

## DOES MIMICRY OF ANT'S REDUCE PREDATION BY WASPS ON SALTICID SPIDERS?

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A common predator of spiders at Legon, Ghana, is the wasp *Pison xanthopus*, 96% of whose prey were salticids. The data from cells built by 31 wasps containing over 800 spiders are used to examine whether mimicry of ants gives protection against *Pison*. Comparison of salticids in wasp cells with those found on nearby vegetation shows that fewer ant mimics (*Myrmarachne* spp.) are taken than one would expect if wasps were capturing salticids in proportion to their occurrence, but also that some individual wasps specialize in capturing *Myrmarachne*. Implications for the searching image hypothesis are discussed. □ *Batesian mimicry, ant-mimicry, Salticidae, predation, search image, Pison, Myrmarachne.*

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Ant mimicry has evolved in several spider families, e.g. Salticidae, Clubionidae, Thomisidae, Aphantochilidae and Theridiidae (Hingston, 1927; Mathew, 1954; Reiskind and Levi, 1967; Reiskind, 1977; Edmunds, 1974, 1978; Wanless, 1978; Oliveira and Sazima, 1984, 1985; Oliveira, 1988). Some of the most precise morphological and behavioural resemblances to ants occur in the salticid genus *Myrmarachne* which is widespread in both the Old and New Worlds, especially in the tropics (Wanless, 1978). At Legon, Ghana, three species of *Myrmarachne* are common, each one closely resembling one species of ant when it is full grown but a different ant species when it is immature (Edmunds, 1978). This mimicry could have two advantages for the spider:

1. It could deceive the ants and so enable the spider to creep up and prey on them. This is aggressive mimicry as may possibly occur in the thomisid *Ameyciaea forticeps* (Mathew, 1954), and is well documented for the aphantochilid *Aphantochilus rogersi* (Oliveira and Sazima, 1984);
2. It could deceive a predator into mistaking it for an ant which that particular predator does not eat. This is batesian mimicry.

*Myrmarachne* do not normally attack ants, so there is no support for aggressive mimicry (Edmunds, 1978; Wanless, 1978). Indeed whenever an ant comes near they use their acute eyesight and quick reactions to avoid contact. This suggests a danger of being killed if caught by the ants (Edmunds, 1978; Wanless, 1978). Direct evidence supporting batesian mimicry is sparse. Edmunds (1974, 1978) argued that because few insectivorous birds prey on ants, the ant mimics

associated with them would also escape predation. He further attempted to show that ant-mimicking spiders are less often taken by the wasp *Pison xanthopus* than are other salticids, but there were rather little data available at that time. More recently, the American ant mimic *Synageles occidentalis* was found being preyed on much less than are non-mimicking salticids by the philodromid *Tibellus oblongus*, and the large salticid *Phidippus clurus* ignored or avoided *Synageles* and ants in exactly the same way, while continuing to attack non-mimicking salticids (Cutler, 1991).

More data on the prey of *Pison xanthopus* are given here to test the theory that ant mimicry gives protection against spider-hunting wasps.

### MATERIAL

Mud cells of *Pison xanthopus* were collected from window frames at the University of Ghana, Legon, Ghana between 1969 and 1973. Individual wasps build from 1-6 cells in a row. Each cell is stocked with 5-10 paralysed salticid spiders and an egg is laid on one of these. The spiders were preserved in alcohol and identified, usually to genus or species. They were also classed as either good ant mimics (*Myrmarachne*), poor ant mimics (*Cosmophasis* sp.) or non-mimics (other genera). Most of the spiders are now in the collection of the Natural History Museum, London. Identification of the spiders was confirmed by F.R. Wanless, and the wasp was determined by the late Professor O.W. Richards.

Spider	Habitat					In wasp cells
	Leaf litter	Short grass	Long grass	Shrubs	Tree trunks	
<b>Good ant mimics</b>						
<i>Myrmarachne foenisex</i> Simon				+	+	+
<i>Myrmarachne elongata</i> Szombathy			+	+		+
<i>Myrmarachne legon</i> Wanless				+		+
<i>Myrmarachne uvira</i> Wanless				+		
<b>Poor ant mimics</b>						
<i>Cosmophasis</i> sp.		+	+	+	+	+
<b>Non-mimics</b>						
<i>Thyene</i> sp.			+	+	+	+
<i>Hyllus</i> sp.			+			
<i>Stenoeurillus</i> sp.			+		+	
<i>Rhene</i> sp.					+	+
<i>Cyllobelus rufopictus</i> Simon	+					
<i>Husaricus udansoni</i> (Audouin)		+				
<i>Schenkelia modesta</i> Lessert					+	
<i>Menemerus</i> sp.					+	+
<i>Pseudicius</i> sp.					+	+
<b>Other non-mimicking salticids</b>		+	+			+

TABLE 1. Salticid spiders in five habitats at Legon, May-July 1973.

### RATIONALE

If ant mimicry deceives wasps so that they do not capture ant-mimicking spiders as often as non-mimics, then the proportion of ant mimics to non-mimics should be lower in wasp cells than in the natural environment. If wasps are not deceived then the proportion of ant mimics should be the same. The test of this hypothesis is to compare the incidence of ant mimics in wasp cells with those found in the field.

### WHERE DOES *PISON* HUNT?

First, the wasp's hunting range must be established so that a random sample of salticids can be collected from the same place. *Pison* is small, difficult to follow in flight, and was observed hunting on only a few occasions. Each time it was running and making short flights over leaves of shrubs. It was never observed on the ground or in grass, but as I spent more time examining shrubs than any other habitat, this is not conclusive. I therefore collected salticids from several different habitats at Legon. If the species of spider

taken by wasps correspond with those found in one particular habitat then the wasps are probably hunting in that habitat.

The habitats are: leaf litter; short, regularly cut grass; long grass and herbage; 1-3m high shrubs; and tree trunks. The spectrum of spiders in wasp cells is most similar to those found in shrubs and trees (Table 1). The canopy was not sampled but probably has a similar fauna. However, it is unlikely that the wasps were hunting in short grass, leaf litter or long grass.

## RESULTS

### SPIDERS IN WASP CELLS AND ON SHRUBS

Some variation in the numbers of spiders caught by each wasp (Table 2) is due to the different numbers of cells completed by the wasps when collected. Cells with full grown larvae or pupae were ignored since the spiders in them were reduced to carapace cuticles, but cells with eggs or young larvae contained spiders that were intact and so are included. The spiders caught by each wasp came from 2-9 cells, e.g. on 3 Feb 1973, the first cell contained a pupa, the second a full grown larva, and the third had nine spiders but no egg. The wasp presumably was killed before fully provisioning this cell.

Of 872 spiders found, 837 were salticids (Table 2); 160 were 'good' ant mimics (i.e. *Myrmarachne* spp.), judged by the human eye, and a further 15 can be classed as poor (behavioural) ant mimics (i.e. *Cosmophasis* spp.). In 1973, every shrub in Zoology (twice) and in Botany (once) was searched (see Edmunds, 1978). All salticids found were scored as either a good mimic, a poor mimic or a non-mimic. The differences between types are highly significant ( $\chi^2_{(2)} = 49.04$ ,  $p < 0.001$ ; Fig. 1). *Pison* clearly take significantly fewer good ant mimics than they do poor mimics or non-mimics compared with their incidences in the environment.

However, wasps searching by running quickly over vegetation are unlikely to find spiders resting in their retreats beneath or between leaves. So perhaps the comparison should be made between the numbers of spiders in wasp cells and the numbers foraging on leaves (excluding those in retreats). These figures are also given in the upper part of Fig. 1 (the black bars only): 61.9% of spiders on shrubs were good mimics compared with 19.1% in wasp cells. This too is highly significant, again indicating that wasps take many fewer good mimics than poor or non-mimics ( $\chi^2_{(2)} = 64.15$ ,  $p < 0.001$ ). The proportion of poor

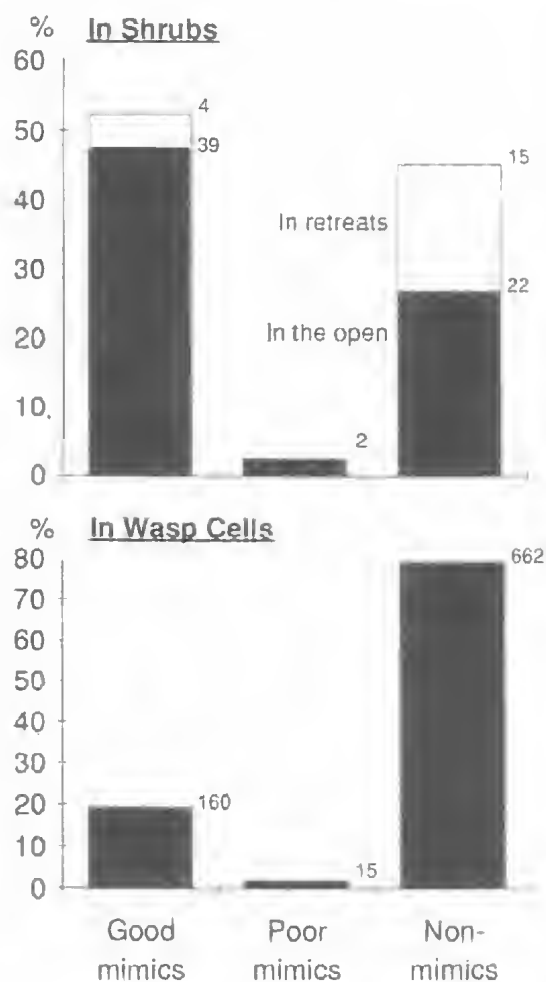


FIG. 1. Comparison of good, poor and non-ant mimicking salticids on shrubs and in cells of *Pison xanthopus*.

mimics taken by wasps is not significantly different from that of the non-mimics, so in the analysis that follows the poor (behavioural) mimic *Cosmophasis* is treated as a non-mimic.

#### SPATIAL OR SEASONAL VARIATION

These comparisons are of spiders on shrubs in February and May 1973 with spiders in wasp cells collected over 3.5 years. The relative numbers of *Myrmarachne* and of other salticids vary throughout the year and over different parts of the University campus, and this may account for the differences in proportions of spider prey taken by wasps. Evidence against this possibility is (1) that there was no significant difference in the relative numbers of *Myrmarachne* and of other salticids

collected on shrubs in February and in May 1973 (Edmunds, 1978); (2) that the three wasp cells (taken 22 Jan- 3 Feb 1973) from close to where the shrubs were surveyed had between them eight *Myrmarachne* and 54 other salticids compared with 24 *Myrmarachne* and 26 other salticids on the shrubs on Feb 2; this difference is highly significant ( $\chi^2_1 = 15.0$ ,  $p < 0.001$ ); and (3) that the data (Table 2) show no clear evidence of spiders occurring at particular sites or in certain seasons. So, while there may be some variation in spider species at different times and places at Legon, such variation is unlikely to account for the very different numbers of salticids taken by wasps assuming that they take different species in proportion to their frequency in the population.

#### NO WASPS NEAR DANGEROUS ANTS

Most *Myrmarachne* taken by *Pison* were black and identified as *M. legon* and *M. elongata* (Wanless, 1978) but some immature specimens could not be identified. Only one specimen of the very common *M. foenisex*, in a total of 160 *Myrmarachne*, was taken. It was a juvenile whose body was red-brown and black (Edmunds, 1978, Fig. 1), quite unlike *Oecophylla*, but very similar to the smaller ant *Crematogaster castanea* which only lives close to *Oecophylla* (Edmunds, 1978). *M. foenisex* closely associates with the aggressive red weaver ant *Oecophylla longinoda*, of similar colour. Adult *M. foenisex* are probably too large for *Pison* to attack, but since it captures many young black *Myrmarachne* one might expect it to take young *M. foenisex* as well. Young *M. legon* are quite similar to young *M. foenisex*, but they do not associate with *Oecophylla* nor with *C. castanea*. Many young *M. legon* but very few *M. foenisex* were taken by *Pison*. Hence, *Pison* probably avoids hunting on plants overrun by *Oecophylla*.

If *Pison* does not hunt on plants with *Oecophylla*, then salticids found with these ants need to be omitted from the comparison of ant mimics and non-mimics on shrubs and in wasp cells (Table 3). Of salticids on shrubs, 49% are good ant mimics compared with 19% in wasp cells. This difference is highly significant, and remains so if spiders in retreats are excluded ( $p < 0.001$ ).

Wasps clearly take fewer *Myrmarachne* than one would predict if they caught them in proportion to their occurrence in the environment. This is therefore good evidence for the defensive value of ant mimicry against predation by *Pison*.

		Mimics		Non-ant mimicking spiders													
Date	Place	My	Co	Ps	Rh	Te	Mc	Vi	So	Th	Sa	Mo	Fi	Os	Of	All	
28.9.69	Zool.				26											26	
29.9.69	Zool.	2		8	1											11	
13.1.71	Bot.	6		29	1											36	
11.2.71	Bot.	34	1		1	6				2	2					46	
12.3.71	Hill	4		44		1	1				1	2				53	
11.4.71	Zool.	1		29										1		31	
19.4.71	Maths			32			1							1		34	
5.2.72	ISSER	15	11	2												28	
15.2.72	Zool.			22					1				3			26	
15.2.72	Zool.	10	2	4					2							18	
18.3.72	Zool.														33 <sup>1</sup>	33	
27.3.72	Zool.	1		24	1											26	
14.4.72	ISSER			36					1							37	
16.5.72	Zool.			20	1											21	
22.5.72	Zool.			28	1			1					1			31	
22.5.72	ISSER			24					1							25	
5.7.72	ISSER			28									2			30	
6.7.72	ISSER	25														25	
1.11.72	Hill	5		36		1		2					1			45	
8.11.72	Zool.	15		16						1						32	
13.11.72	Zool.	8		17	19									1		45	
15.11.72	Zool.	18	1													19	
18.1.73	Hill			26											1 <sup>2</sup>	27	
22.1.73	Bot.	6		25		1		8					2		1 <sup>3</sup>	43	
24.1.73	Bot.	1				9										10	
3.2.73	Bot.	1		5			1			2						9	
13.2.73	Agrie						11									11	
21.2.73	Hill	5		6												11	
23.3.73	Hill	1		33		1	1									36	
27.5.73	ISSER	2		25					1							28	
28.5.73	Agrie.			19												19	
	Total	160	15	538	51	19	15	11	6	5	3	2	9	3	35	872	

TABLE 2. Spiders in cells of *Pison xanthopus* at Legon, Ghana, 1969-1973. Key to Places at University of Ghana, Legon: Faculty of Agriculture, Agric.; Depart. of Botany, Bot.; Institute of Statistical, Social and Economic Research, ISSER; 36 Legon Hill, Hill; Depart. of Mathematics, Maths; Depart. of Zoology, Zool. <sup>1</sup> - 17 Thomisidae, 6 Theridiidae, 5 Clubionidae, 2 Oxyopidae, 1 Araneidae. 1 Selenopidae, 1 Philodromidae. <sup>2</sup> - Oxyopidae. <sup>3</sup> - Gnaphosidae. Taxon head is abbreviated in order: My, *Myrmarachne* sp.; Co, *Cosmophasis* sp.; Ps, *Pseudicius* sp.; Rh, *Rhene* sp.; Te, *Telamonia* sp.; Mc, *Menemerus* sp.; Vi, *Viciria* sp.; So, *Sonoita lightfooti*; Th, *Thyene* sp.; Sa, *Saitis* sp.; Mo, *Mogrus* sp.; Fi, Fissident sp.; Os, other Salticidae; Of, other spider families.

#### DO INDIVIDUAL WASPS HUNT SPECIFIC PREY?

All wasps do not take a similar spectrum of spiders, but each individual preys on one or two species of spider (Table 2). Thus the first wasp in the table preyed on *Rhene* sp., the second and third on *Pseudicius* sp. and the fourth on black species of *Myrmarachne*. Ant mimicry was obviously of defensive value against the first three

wasps who between them took only eight *Myrmarachne* out of 73 spiders (11%), while it failed to protect them from the fourth wasp which took 34 *Myrmarachne* out of 46 prey (74%). Overall, 25 individual wasps took only 38 *Myrmarachne* out of 693 spiders (5.5%), indicating that they had been deceived by the mimicry. The other seven wasps took 122 *Myrmarachne* out of 179 spiders (68.2%) indicating that they had overcome the defence of mimicry to the extent that they preyed almost exclusively on ant mimics (a wasp on 6 July 1972 took 25 *Myrmarachne* and no other spiders, while in the other six wasps *Myrmarachne* taken were never less than 45%).

For the poor ant mimic, *Cosmophasis*, the 15 spiders taken by wasps (Table 2) represent 1.7% of all salticids taken, or 2.1% excluding *Myrmarachne*. This is less than their relative frequency on shrubs (2.4% of all spiders or 5.1% excluding *Myrmarachne*), but the differences are not significant. However, one wasp (on 5.2.72) caught 11 *Cosmophasis* while all other wasps very rarely took them. Therefore, even poor mimicry of ants appears to give some protection against most wasps,

but occasionally a wasp will specialize on this species, just as other wasps do with *Myrmarachne*.

#### HUNTING BY THE SEARCHING IMAGE METHOD

The term searching image was used to describe the way in which tits (Paridae) collect caterpillars for their young: each bird tends to bring insects

TABLE 3. Percentages of *Myrmarachne* (Myrm) and other salticids on shrubs at Legon, and in cells of *Pison xanthopus*. Figures in brackets are numbers and percentages found in open (i.e. not in retreats).

Source of spiders	N	Myrm	Others	$\chi^2$ (n)
Shrubs-all data	82 (63)	52.4 (61.9)	47.6 (38.1)	46.3 (59.8)
Wasp cells	837	19.1	80.9	
Shrubs-omitting <i>M. foenisea</i> & all spiders with ants <i>Oecophylla</i> & <i>Crematogaster castanea</i>	53 (41)	49.1 (58.5)	50.9 (41.5)	25.5 (34.6)
Wasp cells	836	19.0	81.0	

of predominantly a single species for several days and then to abruptly switch to another species (Tinbergen, 1960). Tinbergen hypothesized that the birds recognised caterpillars by particular characters which they 'assimilated in a kind of learning process' and that in their search for prey they looked for these particular characters. Later authors have used the words 'searching image' and 'search image' interchangeably, but its definition has been refined following Croze (1970), Dawkins (1971), Krebs (1973), Lawrence and Allen (1983) and Guilford and Dawkins (1987). It is now generally understood to mean a perceptual change in a predator that temporarily increases its ability to detect particular cryptic prey which it has recently encountered. Searching image needs to be distinguished from various other types of preference that predators may show for particular prey (Krebs, 1973; Lawrence and Allen, 1983), so it is probable that the behaviour observed by Tinbergen which he called hunting by means of a 'specific searching image' would today not be considered a proven example of searching image behaviour.

Individual *Pison xanthopus* clearly concentrate on one or a few species of prey; is this because it hunts using a searching image or by some other method? In a recent critique of the search image concept Guilford and Dawkins (1987, 1988a,b) argue that all studies purporting to demonstrate searching images can actually be explained better in terms of variation in search rate. They make two predictions which can distinguish between the two hypotheses. First, the search rate hypothesis predicts that mimetic prey should take longer to find than non-mimics, so wasps that have learned to find them will slow down their search rate. The searching image hypothesis makes no such prediction. Second, the searching image hypothesis predicts that because of perceptual specialization, wasps concentrating on one type of prey will ignore others. The search rate

hypothesis makes no prediction about concentration on one prey interfering with finding other prey. These observations do not explicitly test either prediction, but I consider that *Pison* is not hunting by adjusting its search rate because different wasps concentrate on different prey implying that capture of several prey of one species interferes with capture of other species. The two wasps at ISSER on 5th and 6th of July 1972 took very different prey. If they had been hunting simply with different search rates then the first wasp should have taken some *Myrmarachne* while the second should have taken some *Pseudicius*. This total concentration on one species of prey is not easy to explain on the search rate hypothesis.

If *Pison* is not capturing prey by adjusting its search rate, there are at least three other hunting methods that might result in the concentration on particular species of prey shown in Table 2:-

1. Wasps might have some sort of preference for one prey rather than another. This is unlikely if the preference is based on taste because the wasps sting but do not eat the prey.

2. Wasps could be searching in different places:-

a. Individual wasps might search in different microhabitats. If each species of spider lives in a slightly different microhabitat on the shrubs then individual wasps could catch different species of spider. Evidence in favour of this is the wasp on 18 Mar 1972 which concentrated on thomisid and other non-salticid spiders. Because it initially caught some of these spiders it is reasonable to suppose that it learned to hunt in particular areas or in a particular way such that it continued to catch these spiders instead of salticids.

b. Wasps might search in one area before going on to another. If spiders are clumped instead of being randomly spaced, then individual wasps hunting in the same general area could capture different species of spider. I often found two or three spiders of one species on a shrub so the distribution is clumped rather than random. However, there is no exclusion of one species by another, and the clumping may simply be of recently mated pairs or of parents with young that have failed to disperse. This impression has not been quantified, but I consider it unlikely that it could explain the extreme specialization on one species (Table 2).

3. The wasps may have a perceptual searching image as implied by Croze (1970). Wasps of other genera can learn the configuration of landmarks near their burrows (see Tinbergen,

1958), and this presumably involves some perceptual memory not unlike that in ourselves when we search for something with a particular image in our mind.

It is unclear which of the above methods of prey capture or if another method (e.g., Krebs, 1973) is involved. But certainly some such behaviour occurs both in *Pison* and in other wasps, e.g. the sphecid *Chalybion fuscipenne* (J. Edmunds, 1990).

### CONCLUSIONS

Clearly, ant-mimicking spiders are common, more so than non-mimics in some habitats. Ant mimicry may give protection against wasps such as *Sceliphron* which prey on spiders of various families (Edmunds, 1974; J. Edmunds, 1990). The results confirm the suggestion from a preliminary, less rigorous study (Edmunds, 1974), that ant mimicry is of protective value against the specialist predator *Pison xanthopus*. The evidence that behavioural ant mimicry protects *Cosmophasis* against *Pison* is not conclusive; it may be protective against other wasps or against birds. Wanless (1978) and Curtis (1988) have evidence that spiders of this genus prey on ants, so this mimicry could also be aggressive rather than defensive in function.

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